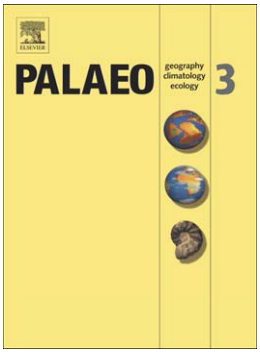

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PII: S0031-0182(13)00069-2
DOI: doi: 10.1016/j.palaeo.2013.01.025
Reference: PALAEO 6405

To appear in: *Palaeogeography, Palaeoclimatology, Palaeoecology*

Received date: 2 November 2012
Revised date: 21 January 2013
Accepted date: 31 January 2013

Please cite this article as: Álvarez-Lao, Diego J., Arsuaga, Juan L., Baquedano, Enrique, Pérez-González, Alfredo, Last Interglacial (MIS 5) ungulate assemblage from the Central Iberian Peninsula: The Camino Cave (Pinilla del Valle, Madrid, Spain), *Palaeogeography, Palaeoclimatology, Palaeoecology* (2013), doi: 10.1016/j.palaeo.2013.01.025

Last Interglacial (MIS 5) ungulate assemblage from the Central Iberian Peninsula: The Camino Cave (Pinilla del Valle, Madrid, Spain)

Diego J. Álvarez-Lao [a,*], Juan L. Arsuaga [b,c], Enrique Baquedano [d], Alfredo Pérez-González [e]

[a] Área de Paleontología, Departamento de Geología, Universidad de Oviedo. C/ Jesús Arias de Velasco, s/n, 33005 Oviedo, Spain.

[b] Centro Mixto UCM-ISCIII de Evolución y Comportamiento Humanos. C/ Sinesio Delgado, 4, 28029 Madrid, Spain

[c] Departamento de Paleontología, Facultad de Ciencias Geológicas, Universidad Complutense de Madrid. Ciudad Universitaria, 28040 Madrid, Spain

[d] Museo Arqueológico Regional de la Comunidad de Madrid. Plaza de las Bernardas, s/n, 28801-Alcalá de Henares, Madrid, Spain

[e] Centro Nacional de Investigación sobre la Evolución Humana (CENIEH). Paseo Sierra de Atapuerca, s/n, 09002 Burgos, Spain

* Corresponding author: dalao@geol.uniovi.es Telephone: 0034 985103143

Fax: 0034 985103103

Abstract

The fossil assemblage from Camino Cave, corresponding to the late MIS 5, constitutes a key record to understand the faunal composition of Central Iberia during the last Interglacial. Moreover, the largest Iberian fallow deer fossil population was recovered here. Other ungulate species present at this assemblage include red deer, roe deer, aurochs, chamois, wild boar, horse and steppe rhinoceros; carnivores and Neanderthals are also present. The origin of the accumulation has been interpreted as a hyena den.

Abundant fallow deer skeletal elements allowed to statistically compare the Camino Cave fossils with other Pleistocene and Holocene European populations. The morphological comparison of the dentition and morphometrical analyses of the metapodials suggest that the fallow deer from Camino Cave are closer to the subspecies *Dama dama geiselana* and *Dama dama tiberina* than to the recent *Dama dama dama*.

Estimations of the age at death in several fallow deer young individuals provided information on seasonality, suggesting that the cave was occupied by the hyenas almost all year round.

The ungulate composition provides a clear example of an interglacial faunal complex which agrees with the published pollen, charcoal and small vertebrate data that indicate a continental Mediterranean climate. This interglacial character was also registered at other Iberian MIS 5 sequences coming from the Mediterranean margin.

Keywords:

Early Late Pleistocene; MIS 5c; Fallow deer; *Dama dama* cf. *geiselana*; Morphometry; Palaeoenvironment

1. Introduction

Marine Isotope Stage (MIS) 5, often referred to as the last interglacial *sensu lato*, was a period of minimum ice volume that expanded from c. 130 to 75 ka BP (Sánchez Goñi, 2007). This period was first defined by Harting (1852), who called it Eemian. This term, equivalent to the Ipswichian (for the Birtish Isles) or Riss-Würm (for the Alps), is widely used by many authors to refer to the last interglacial. Shackleton (1969), based on the correlation between marine and terrestrial records, proposed that only the first ^{18}O minimum values of MIS 5, named MIS 5e, had to be considered the equivalent of the Eemian as identified on land (Sánchez Goñi, 2007). Analyses of pollen, dinocyst and

isotopic data from marine sediments of the Iberian marine margin indicate that North Atlantic sea surface temperatures were in phase with Iberian climate during the Last Interglacial (Sánchez Goñi et al., 1999).

The archaeo-palaeontological site of Camino Cave, integrated in the Pinilla del Valle archaeological complex (Madrid, Central Spain, Fig. 1), is located in the mountainous area of the Guadarrama Mountain Range, at 1114 m above sea level. Information regarding geology, stratigraphy, taphonomy and other features of the site is widely discussed by Arsuaga et al. (2012).

Investigations at Camino Cave were first carried out during the 1980s decade (Alférez et al., 1982; Alférez and Iñigo, 1990; Buitrago, 1992). A large amount of fossil remains, along with two human molars (Alférez et al., 1982, Alférez, 1985; Alférez and Iñigo, 1990; Alférez and Roldán, 1992; Buitrago, 1992, Maldonado, 1996) identified as representing Neanderthals (Arsuaga et al., 2010, 2011, 2012), were then recovered. Recent excavations carried out between 2002 and 2009 provided relevant information from archaeological, palaeobotanical, palaeontological, geological and palaeoanthropological points of view (Arsuaga et al., 2012). The origin of the fossil accumulation has been interpreted as a hyena den (Díez, 1993; Arsuaga et al., 2010). A great assemblage of large mammal fossils, mostly ungulates, was recovered during these last field campaigns. The Camino Cave sequence is composed of four sectors (Fig. 2; Arsuaga et al., 2012). Most of the fossils come from the denominated North sector, concretely from the Layer 05, dated by TL (thermoluminescence) to 90.961±7881 ka BP (Pérez-González et al., 2010). Other part of the fossils was recovered in the Central sector. It is assumed that, most probably, fossils from both sectors are of the same or very similar age, although deposited under different sedimentary processes, since they were placed at the same topographic level and there are not significant differences in faunal composition and taxa proportions between them. The faunal assemblage was therefore studied as a whole.

Chronology of the Layer 05 corresponds to MIS 5c, a temperate phase recorded in marine and continental sequences from Europe and Siberia, also known as St. Germain 1 or Börup interstadial (Caspers et al., 2002; Prokopenko et al., 2002; Sánchez Goñi et al., 2005; Müller and Sánchez Goñi, 2007; Rousseau et al., 2007; Väliranta et al., 2009; Laukhin, 2011). However, since the range of the date is wide (± 7881 years) we cat not reject the possibility that the fossil assemblage corresponds to the previous temperate phase, the MIS 5a.

Palaeontological and palaeoenvironmental information from MIS 5 is much less abundant than those corresponding to MIS 3 and 2. Most of this information comes from a number of sites from central and northern Europe (Kolfschoten, 2000; Turner, 2000; Kahlke, 2002; Koenigswald, 2007), whereas at southern Europe this period is less known. A number of works including MIS 5 palaeoenvironmental information from the Iberian Peninsula, inferred from pollen and isotope records from marine and terrestrial sequences, have been published (Zazo et al., 1993; Carrión et al., 1998, 1999; Sánchez Goñi et al., 1999; Carrión García et al., 2000; González-Delgado et al., 2005; Fernández et al., 2007; Muñoz García et al., 2007). Paleontological information from this period at Iberian sequences comes mostly from the Mediterranean margin (Blasco et al., 2008; Fernández Peris et al., 2008; Daura et al., 2010; Rosell et al., 2010a, Fig. 1) while in Central Iberia it remained insufficiently well-known. The fossil assemblage of Camino Cave is therefore of special interest because it constitutes the most complete non-Mediterranean Iberian record corresponding to the last interglacial, providing relevant information on the paleontological, palaeoecological and paleoenvironmental conditions of Central Iberia during MIS 5.

This work provides a paleontological description and analysis of the ungulate fossil remains with special attention to the fallow deer (*Dama dama*) population, the largest assemblage of this species in the Iberian Peninsula.

2. Material and methods

Ungulate remains from Camino Cave are generally well preserved, most probably related to the non-anthropic origin of the bone accumulation. Consequently, a high proportion of the remains (around 60 % of the fragments larger than 3 cm) resulted taxonomically identifiable.

A total of 1235 ungulate remains were recovered from the 2002-2009 field works and are here analysed (Table 1). These fossils correspond to the species *Dama dama* (fallow deer), *Cervus elaphus* (red deer), *Capreolus capreolus* (roe deer), Bovini cf. *Bos primigenius* (aurochs), *Rupicapra rupicapra* (chamois), *Sus scrofa* (wild boar), *Equus caballus* (horse) and *Stephanorhinus hemitoechus* (steppe rhino). A significant proportion of the ungulate bone fragments (22.9 %), corresponding either to fallow deer or red deer, were impossible to classify to a single species, so they are generically classified as *Dama/Cervus*. Carnivores, not considered in this study, are represented by the following species: *Canis lupus, Vulpes vulpes, Ursus arctos, Mustela putorius, Mustela nivalis, Crocuta crocuta, Lynx* cf. *pardinus, Felis silvestris, Panthera leo* and Felidae indet. (*Panthera pardus* size) (Arsuaga et al., 2012). Measurements are taken following the standards of Driesch (1976) for artiodactyls and equids, and Guérin (1980) for rhinoceroses. All measurements are given in millimetres. The age at death of *Dama dama* juvenile individuals was estimated following Brown and Chapman (1990). Morphometrical data were compared with an extensive sample, mainly coming from Western Europe, published by Altuna (1971, 1972, 1976), Leonardi and Petronio (1976), Pérez Ripoll (1977), Castaños (1980), Guérin (1980), Soto and Meléndez (1981), Delpech (1984, 1988), Lister (1986), Mariezkurrena and Altuna (1989), Di Stefano and Petronio (1997), Pfeiffer (1998), Altuna and Mariezkurrena (2000), Liouville (2007), and Auguste (2010).

The fossils are stored at the Museo Arqueológico Regional de la Comunidad de Madrid (Alcalá de Henares, Madrid).

3. Systematics: description of the remains and discussion

3.1. Order Artiodactyla Owen, 1848

3.1.1. Family Cervidae Goldfuss, 1820

The ungulate assemblage from Camino Cave is dominated by cervids (Family Cervidae), constituting 83.4 % of the ungulate remains (Fig. 3a-i, Table 1). The most abundant species is fallow deer (*Dama dama*) followed by red deer (*Cervus elaphus*) and, in a low proportion, roe deer (*Capreolus capreolus*) (Table 1).

Dama dama Linnaeus, 1758

Fallow deer is the dominant species in the Camino Cave assemblage, constituting 51.5 % of the ungulate remains (Fig. 3a-d, Table 1). Teeth are the most abundant remains although all anatomical elements are present. Among the limb bones, metapodials are abundant and some of them are preserved in good conditions. A number of humerus, radius and tibia fragments were also recovered. Phalanges and carpal and tarsal bones are also relatively abundant. All age groups are represented, from very young specimens (around three months of age) to very old ones, which provides relevant information on seasonality (section 4).

Fallow deer fossils from the 1980s excavations of Camino were firstly assigned to the species *Dama clactoniana* (Buitrago, 1992). Subsequently, Made (2001) and Made et al. (2003) included these remains in the subspecies *D. dama geiselana* based on dentition size.

Dentition of fallow deer from Camino Cave shows the morphology and size typical of the genus *Dama*. Cingulum is slight or absent in upper molars and is not denticulate. Upper premolars show a lingual sulcus between protocone and hypocone, which is very deep in P^2, slighter in P^3 and almost absent in P^4. This feature (molarization) is also typical of the genus *Dama* (Lister, 1996; Pfeiffer, 1998; Di Stefano and Petronio,

2002). Protoconal fold of P^4 occasionally produces a small fossette in worn out specimens (Fig. 3a). The lingual wall is sloping about 45º or even less (with respect to the base of the molar) in the upper dentition and especially in P^4. Lister (1986) observed that the metaconid may fuse with the entoconid quite high in the P_3 crown in a number of *D. dama clactoniana* specimens from Swanscombe and Riano, whereas they are never fused in recent *D. dama*. In P_3 of *D. dama tiberina*, an early subspecies of *D. dama* from the MIS 7 of Italy, these elements are always unfused (Di Stefano and Petronio, 1997). Also in *D. dama geiselana* from Neumark Nord, figured by Pfeiffer (1998), the fusion between metaconid and entoconid is absent in P_3, as well as in all preserved P_3 from Camino Cave (Fig. 3b). Therefore, P_3 from Camino are not comparable with *D. dama clactoniana* in this feature.

Antler morphology is considered one of the most systematically significant features in the genus *Dama* for identification at subspecies level (Leonardi and Petronio, 1976). Unfortunately, only basal and beam fragments have been recovered at Camino Cave, so we assume that identification to subspecies level is here difficult.

Dentition measurements are not here considered for systematics because teeth, especially upper molars, show great variability in length, since many specimens are affected by a strong interdental attrition (which reduces their length considerably). This feature is typical of mature or old individuals.

Postcranial elements are here considered for systematic purposes. As above indicated, metapodials (Fig. 3c-d) are the most abundant and better preserved postcranial elements at Camino Cave. A total of seven complete metacarpals and nine complete metatarsals were recovered (fossils from the 1980s excavations have also been included). The dimensions of these elements (Table 2) were compared with a sample of *D. dama geiselana* from Neumark Nord (Type Locality), *D. dama tiberina* from several Italian sites and modern *D. dama dama* (Fig. 4-5, Table 2).

Differences in limb bones between *D. dama geiselana* and the modern *D. dama dama* not only affect their size (the former species is about 15 % larger) but also their

proportions (Pfeiffer, 1998). The metapodials of *D. dama dama* are proportionally shorter and broader than those of *D. dama geiselana* and *D. dama tiberina* as can be seen in Fig. 4-5, where two separated populations can be clearly recognised.

In order to compare morphometrically the Camino population with the three cited fallow deer subspecies *D. dama dama*, *D. dama geiselana* and *D. dama tiberina* we selected the metapodials, which are the most frequently preserved postcranial elements, for statistical analyses. Data were collected from the type population of *D. dama geiselana* (Neumark Nord), from a sample of recent *D. dama dama* (both published by Pfeiffer, 1998), and from Italian *D. dama tiberina* specimens (only data on metatarsals are available) published by Di Stefano and Petronio (1997).

The simultaneous comparison of the two metapodial morphometric variables among the samples was carried out by means of analysis of covariance (ANCOVA) (Quinn and Keough, 2002) using the program PAST version 2.15 (Hammer et al., 2001). The variable PW (proximal width) has been compared among the three populations, taking the variable L (maximum length) as covariate. Homogeneity of slopes was tested previously to the ANCOVA.

For metacarpals, the three populations (data *from D. dama tiberina* was not available) showed homogeneity of slopes in their regression lines ($p = 0.112$). The ANCOVA showed differences between the mean values of the three populations when the effect of the covariate was removed ($F_{2, 71} = 19.2$; $p = 2.165 \times 10^{-7}$). Metacarpals from Camino Cave fallow deer were clearly related to *D. dama geiselana* from Neumark Nord (Fig. 4). The scatterplots of both populations overlapped partially and regression lines were statistically not differentiable, with Camino specimens merely following the *D. d. geiselana* line in its lower end. Metacarpals from Camino Cave were proportionally longer (i.e. greater Length/Width ratio) than those of the *D. d. dama* sample, and therefore both populations were well separated (their scattering plots do not overlap and their regression lines are statistically different).

For metatarsals the results were very similar as for metacarpals. Slopes were homogeneous (p = 0.902). ANCOVA indicated also that there are differences among the mean values of PW from the three populations when the effect of the covariate (L) was removed ($F_{3,85}$ = 11.08; p = 3.278 x 10^{-6}). Regression lines showed a very similar pattern for the metatarsals as for the metacarpals (Fig. 5). Camino specimens, *D. d. geiselana* and *D. dama tiberina* had a similar regression line (although Camino specimens are smaller than the other two populations) and significantly different from the *D. d. dama* sample. The scatterplot of Camino Cave metatarsals overlapped partially with *D. d. geiselana* but do not overlapped with *D. d. tiberina*, which are larger in size. This suggests that Camino fallow deer are more comparable with *D. d. geiselana*.

Some authors (Kurtén, 1968; Lister, 1986; Di Stefano and Petronio, 2002) indicated that fallow deer from European Late Pleistocene are like the recent specimens, belonging to the subspecies *D. d. dama*, while for Made et al. (2003) MIS 5 fallow deer are intermediate between *D. d. geiselana* and *D. d. dama*. The lack of complete fallow deer antlers in Camino Cave prevents an accurate identification at sub species level; however, postcranial elements suggest that specimens from Camino Cave are closer to the MIS 7 subspecies *D. d. geiselana* and *D. d. tiberina* than to the modern *D. d. dama*. In particular, size is more similar to *D. d. geiselana*. The smaller size of the Camino population can be related to the trend of decreasing size registered in the genus *Dama* from MIS 11 (Made et al., 2003), considering that Camino Cave assemblage is about 100 ka younger than those providing *D. d. geiselana* and *D. d. tiberina* fossils (Di Stefano and Petronio, 1997; Mania et al., 2003; Made, 2010).

Cervus elaphus Linnaeus, 1758

Red deer is the second species in abundance in the Camino Cave assemblage, making up 8.4 % of the ungulate remains (Fig. 3e-h, Table 1). Almost all skeletal elements are preserved, especially teeth and metapodial fragments. Antler basal

remains are also frequent, showing different development stages. The lack of well-preserved antlers prevents taxonomic identification at subspecies level. Metapodials and M_3 (a dental element which is not affected by attrition) are the most numerous elements from Camino and were compared with a sample of Pleistocene red deer from Western Europe (Table 3). Specimens from Northern Iberia (sites of Lezetxiki, Aitzbitarte IV, Urtiaga, Tito Bustillo, Zatoya, Labeko Koba, La Paloma and Las Caldas) corresponding to the last cold stage (MIS 3 and 2) are visibly larger in size than those from Camino Cave. Specimens from Swanscombe and Cova Negra, both from temperate stages (MIS 7 and 5, respectively), are more similar in size to those from Camino Cave. These data suggest that populations from cold stages are larger in body size than those from temperate phases, as was previously observed by authors like Mariezkurrena and Altuna (1983) for Iberian red deer. These size differences might reflect either Bergmann's rule (cold climate selects for survival of larger body sizes) or perhaps differences in available resources under different environmental conditions: high quality vegetation from the cold stages favoured ruminants like the red deer and allowed them to reach a larger body size (Guthrie, 1990).

Dama/Cervus

As previously indicated, a significant proportion of the ungulate bone fragments (22.9 %, Table 1), corresponding to either fallow deer or red deer, have been classified as *Dama/Cervus*, since it was impossible to classify them to a single species.

Capreolus capreolus Linnaeus, 1758

Roe deer remains are very scarce, contributing only 0.6 % of the ungulates (Fig. 3i, Table 1). These are one mandible fragment and four isolated lower teeth likely corresponding to one single specimen. Comparative studies are not possible since no postcranial elements are available.

3.1.2. Family Bovidae Gray, 1821

Bovini cf. *Bos primigenius* Bojanus 1827

Bovine remains comprise 5.5 % of the ungulate assemblage (Table 1). Teeth remains correspond almost exclusively to upper dentition (Fig. 3j), which are not the most reliable diagnostic elements to distinguish between both bovine taxa (*Bos* and *Bison*). The postcranial remains consist principally on carpal and tarsal bones (Fig. 3k). Limb bones are fragmented and not measurable, which prevents any comparative study. Hence, there are not enough criteria preserved for to allow an accurate taxonomic identification of the bovines. However, some diagnostic elements such as metacarpals were recovered during the 1980's field works and studied by Buitrago (1992). The morphology of three metacarpals (figured by Buitrago, 1992) shows that the lateral edges are clearly divergent towards the distal end (in anterior view) which, following the criteria of Stampfli (1963), is an indicative feature of *Bos primigenius*. One M_3, also studied and figured by Buitrago (1992), shows the hypoconulid drawing a wide angle with the hypoconid (in occlusal view), which is admitted by Koken (1885) and Stampfli (1963) as a typical feature of *Bos primigenius*. By these reasons, it is assumed that bovine remains from the recent excavations belong most probably to aurochs (*Bos primigenius*).

Rupicapra rupicapra Linnaeus, 1858

One isolated M_3 (Fig 3l) constitutes the single evidence of chamois in Camino Cave, representing 0.1 % of the ungulate assemblage (Table 1). The presence of this species in the assemblage is of great interest from a palaeoenvironmental point of view (section 5).

3.1.3. Family Suidae Gray, 1821

Sus scrofa Linnaeus, 1858

Wild boar remains comprise 2 % of the ungulate assemblage (Fig. 3m, Table 1). Fossils consist mainly of dentition whereas postcranial remains are limited and fragmented. The sample is too small for to allow comparative studies.

3.2. Order Perissodactyla Owen, 1848

3.2.1. Family Equidae Gray, 1821

Equus caballus Linnaeus, 1758

Horse remains constitute 7.6 % of the ungulates (Table 1). The material consists of teeth and some postcranial elements, mainly metapodials, phalanges and carpal/tarsal bones (Fig. 3n-p). Since most of the postcranial elements are fragmented, only a limited number of measurable specimens per element are available. Morphometrical information is therefore scarce and not representative enough for comparative studies. The morphology of the upper dentition is typical of the caballine equids, with a large protocone, concave surfaces between styles, intense folding in the enamel of the fossettes and a well developed caballine fold.

Horse remains from the 1980's excavations of Camino Cave, more abundant and well preserved, were studied by Maldonado (1996), who classified them as belonging to the subspecies *Equus caballus torralbae* based on tooth morphology and body size. Morphology and measurements of the fossils from the recent excavations are not different to the ones published by Maldonado (1996).

3.2.2. Family Rhinocerotidae Owen, 1845

Stephanorhinus hemitoechus Falconer, 1868

Rhinoceroses comprise 1.4 % of the ungulates (Table 1). The most taxonomically diagnostic element is a well preserved upper molar (M^1 or M^2, Fig. 3q), whereas

postcranial remains are very scarce and fragmented. The metaloph and protoloph of the upper molar are separated by a deep “valley”, so they remain unfused except at the crown’s base, in the lingual side. Other features of this molar are the presence of an open mediofossette, a crista, a single crochet and relatively thin enamel with slight roughness. All these features are typical of the genus *Stephanorhinus* and different of *Coelodonta*, the other genus of Late Pleistocene European rhinoceroses (Guérin, 1980). The stage of wear is advanced, showing a well developed postfossette. The presence of crista and the lack of protocone constriction in this specimen are typical features of the two Late Pleistocene *Stephanorhinus* species (*S. hemitoechus* and *S. kirchbergensis*) following Lacombat (2006). Moreover, the presence of a prominent paracone fold in this molar can be considered a distinctive feature for *S. hemitoechus*, significantly different of *S. kirchbergensis* which shows light curling without a marked relief in the vestibular wall of the upper molars (Lacombat, 2006). For these reasons, we classify this specimen into the species *Stephanorhinus hemitoechus* (steppe rhino), which is a relatively frequent species of the Iberian Middle and Late Pleistocene (Cerdeño, 1990). Measurements suggest that it correspond to an M^2 (Table 4), compared with a sample from Western Europe published by Guérin (1980).

4. Seasonality

The presence of different age stages in juvenile individuals of *Dama dama geiselana* provides interesting information in order to estimate in which period of the year the cave was occupied by predators (mostly hyenas). Nineteen of the individuals died during their first 22 months of life, which allows us to know with high precision the age of death based on teeth wear, following Brown and Chapman (1990). Considering that fallow deer births occur between end of May and June (Corbet and Ovenden, 1980) it is possible to estimate with relatively high accuracy the month of death (Fig. 6). The results suggest that the cave was occupied by hyenas throughout almost all the year,

with a small hiatus between May and June. It must be considered the possibility that this hiatus probably reflects a lack in the fossil record.

The degree of development in antlers can also provide information on seasonality. Deer antlers from Camino Cave show different development stages (shed antlers, skull fragments with antlers starting to grow and skull fragments with full developed antler bases, Fig. 3g-h), which agrees with the idea that the cave was occupied by predators during most of the year.

5. Palaeoenvironmental context

The ungulate assemblage from Camino Cave represents a typical example of an interglacial faunal complex. Similar faunal associations including *Dama dama*, *Cervus elaphus*, *Bos primigenius* and *Stephanorhinus hemitoechus* are found in a number of European last interglacial sites, such as Barrington, Trafalgar Square, Taubach and Burgtonna I (Stuart, 1982, Kolfschoten, 2000; Kahlke, 2002).

Fallow deer environmental preferences are forested areas, from dense deciduous and coniferous forests to open woodlands (Guérin and Pathou-Mathis, 1996). The reason of such fallow deer abundance in the Camino Cave assemblage could be related with the presence of Mediterranean vegetation, which was indicated by pollen and charcoal analyses: *Pinus* was the most abundant element, accompanied in lesser proportions by evergreen and deciduous *Quercus*, *Corylus*, Oleaceae, *Betula* and also riparian taxa as *Alnus*, *Salix* and *Ulmus* (Arsuaga et al., 2012). In addition, microvertebrate analyses include several typically thermophilous species, as *Hystrix* cf. *brachyura, Microtus cabrerae, Microtus* gr. *duodecimcostatus, Crocidura russula, Testudo hermanni, Coronella* cf. *girondica* and *Pelobates cultripes* (Arsuaga et al., 2012), which is also consistent with the presence of *D. dama*.

The ungulate association at Camino Cave suggests an environmental complex composed of, at least, three different ecosystems: forested areas, indicated by the

presence of *Dama dama,* Bovini cf. *Bos primigenius, Sus scrofa* and *Capreolus capreolus*; open grasslands, evidenced by the presence of *Equus caballus* and *Stephanorhinus hemitoechus*; and rocky high mountain areas, indicated by the alpine species *Rupicapra rupicapra*. These three different environments can still be seen nowadays in the surroundings of the cave.

6. Fallow deer in the Iberian Pleistocene

The Camino Cave fossil assemblage is of special interest in the Iberian Peninsula given its high proportion of *Dama dama* remains (51.5 % of the ungulate remains), and because it constitutes one of the most recent known Iberian assemblages of this species.

6.1. European context

The fallow deer lineage (genus *Dama*) was widespread throughout Europe from Lower Pleistocene to Late Pleistocene (Leonardi and Petronio, 1976). Fossils of this genus have been recovered in numerous sites from Germany, France, the British Isles, Poland, Italy and the Iberian Peninsula (Kurtén, 1968; Bouchud, 1972; Leonardi and Petronio, 1976; Cregut, 1979; Stuart, 1982; Kahlke, 2002).

Since the Middle Pleistocene, fallow deer occurrences are normally associated to interglacial faunal complexes. A number of sites of Holsteinian age (MIS 11), such as Bilzingsleben, Swanscombe and Clacton, yielded fossil assemblages with high proportions of *Dama dama clactoniana* remains along with other typical interglacial taxa like *Stephanorhinus hemitoechus, Equus, Sus scrofa* and *Cervus elaphus* (Stuart, 1982; Made, 1998; Kahlke, 2002). The German site of Neumark Nord, corresponding to an Intra-Saalian warm period equivalent to MIS 7 (Made, 2010), is of special interest because the largest known assemblage of fallow deer fossils (80 more or less

complete skeletons), corresponding to the subspecies *Dama dama geiselana*, was recovered here (Pfeiffer, 1998). The ungulate assemblage from this site also includes *Stephanorhinus kirchbergensis*, *Cervus elaphus* and *Bos primigenius* (Kolfschoten, 2000). Contemporary with Neumark Nord, MIS 7 Italian sites provided the subspecies *Dama dama tiberina* (Di Stefano and Petronio, 1997). During the following and last interglacial (MIS 5), contemporary with Camino Cave, fallow deer is present in many sites from Central and Southern Europe and the British Isles, like Barrington, Trafalgar Square, Swanton Morley, Taubach, Burgtonna, Rheinsande, Lehringen, Grobern1, Fontéchevade and Bolomor (Stuart, 1982; Fernández Peris et al., 1999; Kolfschoten, 2000; Kahlke, 2002; Koenigswald, 2007; Chase at al., 2007). In Italy, fallow deer are still widespread at the beginning of the Late Pleistocene (Sardella et al., 2005). Subsequently, when the cold and dry environmental conditions of the last glacial (corresponding to MIS 4–MIS 2 interval) arrived, fallow deer disappeared from most of Europe, limiting their distribution to Mesopotamia and Asia Minor, where they still survive nowadays (Kurtén, 1968).

6.2. The genus Dama in the Iberian Pleistocene record

Fallow deer species have been registered in Iberia during the Lower, Middle and early Late Pleistocene.

Lower Pleistocene Iberian sites: Lachar and Fuensanta provided *Dama* cf. *nestii* remains (Aguirre, 1989). Fallow deer from TD4-6 layers in Atapuerca are classified as *Dama nestii vallonetensis* by Made (2001). Arribas et al. (2001) identified *Dama* cf. *nestii* at Fonelas and *Dama rhenana/Dama nestii* in Huélago-1, La Puebla de Valverde, Venta Micena and, doubtfully, in Fuente Nueva-3, Quibas and Huescar-1 sites. *Dama* sp. is noticed in Cueva Victoria (Gibert Clols et al., 2006). Fallow deer from Cortijo de las Nieves are classified as *Praedama savini* by Ruiz-Bustos et al. (1990).

Middle Pleistocene Iberian sites: fallow deer from Torralba and Ambrona are mentioned by Aguirre (1989) as belonging to the species *Dama* sp. cf. *clactoniana*, whereas Sesé and Soto (2005) identified *Dama* cf. *dama* at Ambrona. *Dama* sp. was found in Middle Pleistocene layers from Solana de Zamborino (Aguirre, 1989), Bolomor Cave (Sanchis Serra and Fernández Peris, 2008), Mollet Cave (Solés and Maroto, 2002; Maroto et al., 2012) and Valdocarros site (Yravedra and Domínguez-Rodrigo, 2009; Sesé et al., 2011; Blain et al., 2012). *Dama* cf. *clactoniana* is also mentioned in Villacastín (Arribas, 1994). TD10-11 and TG10-11 layers from Atapuerca provided *Dama dama* aff. *clactoniana* (Made, 2001).

Late Pleistocene Iberian sites: the fossil record suggests that fallow deer persisted in the Iberian Peninsula until the early Late Pleistocene, previous to the environmental cooling of the last glacial episode. Along with Camino Cave, Late Pleistocene fallow deer occurrences from the Iberian Península (cited as *Dama dama* or *Dama* sp.) come from Bolomor Cave (Blasco et al., 2008, Blasco and Fernández Peris, 2010), Teixoneres Cave (Rosell et al., 2010a), Cova del Rinoceront (Daura et al., 2010), Cova Negra (Martínez Valle, 2009) and Las Yedras (Ruiz Bustos 1978). Percentages of fallow deer remains are variable in Iberian fossil assemblages, but no other Iberian site reached values as high as those from Camino Cave.

7. The Iberian Peninsula during MIS 5

MIS 5 Iberian sequences are scarce and come mainly from the Mediterranean margin. Besides Camino Cave, significant faunal assemblages from this episode are only known from four other Iberian sites (Fig. 1), described below. Faunal composition indicates, in every case, temperate environmental conditions.

-The Bolomor Cave (Valencia) stratigraphic sequence includes some layers (VII to I) that correspond to MIS 5, with one absolute date of 121 ka (Blasco et al., 2008, Blasco and Fernández Peris, 2010). Ungulate species are dominated by *Cervus elaphus*,

Dama sp., *Equus ferus* and, at lower percentages, *Paleoloxodon antiquus*, *Hippopotamus amphibius*, *Hemitragus* sp., Bovinae indet. and *Stephanorhinus hemitoechus* (Blasco et al., 2008). The presence of other environmentally indicative vertebrates such as *Macaca sylvanus* and *Testudo hermanni* is also reported (Blasco, 2008; Blasco and Fernández Peris, 2010).

-Level III of Teixoneres Cave (Barcelona) is placed over a stalagmitic bed dated between 100 and 94 ka BP (Rosell et al., 2010b). Combination of three rodent species (*Pliomys lenki, Hystyx* sp. and *Microtus (Iberomys) cabrerae*) suggests a chronology between 90 and 60 ka BP for this level (López-García et al., 2012), likely contemporary with Camino Cave. The ungulate assemblage is represented by *Cervus elaphus*, *Equus ferus*, *Bos primigenius*, *Capreolus capreolus* and *Sus scrofa* (Rosell et al., 2010b). Termophilus microvertebrates as *Hystrix* sp., *Microtus (Iberomys) cabrerae* and Testudinae are also present at this assemblage (Rosell et al., 2010a, b; López-García et al., 2012).

-At Cova del Rinoceront (Barcelona), level I corresponds to late MIS 5 (Luján and Borràs, 2009; Daura et al., 2010). The most abundant ungulate species are *Cervus elaphus*, *Dama dama* and *Capra* sp., and the presence of Bovinae indet. is also detected (Daura et al., 2010). The tortoise *Testudo hermanni* is present at this level (Luján and Borràs, 2009).

-The statigraphic sequence of Cova Negra (Valencia) includes several levels (XV to XI) that correspond to MIS 5 (Fernández Peris et al., 2008; Martínez Valle, 2009). The scarce faunal remains recovered at these layers include *Cervus elaphus*, *Dama* sp., Caprinae indet., *Equus caballus* and *Stephanorhinus* sp. (Martínez Valle, 2009).

-The HAT site, located in the terrace gravel of the Jarama River (Madrid) has been dated by TL on 74 +16 / -12.1 ka BP, corresponding to the end of the MIS 5 (Panera et al., 2005, 2008; Sesé et al., 2011). The single ungulate species identified at this site is *Equus caballus* (Panera et al., 2005), however, micromammal record included some

termophilus species (as *Microtus cabrerae, Eliomys quercinus* and *Apodemus* sp.) which are indicative of temperate environment (Sesé et al., 2012).

In sum, information from MIS 5 at the Iberian Peninsula comes mainly from the Mediterranean area while there is almost no information from other Iberian regions for the same period. Temperate faunas are dominant during this episode, including the presence of environmentally indicative species like *Dama dama*, *Testudo hermanii* and, occasionally, *Hippopotamus amphibious and Macaca sylvanus*. Therefore, the Camino Cave sequence provides relevant information on MIS 5 from non-Mediterranean Iberian areas.

8. Conclusions

The ungulate assemblage from Camino Cave provides relevant information on the palaeoenvironmental conditions of Central Iberia during MIS 5, since data from this period are very scarce in the Iberian record and come almost exclusively from the Mediterranean margin.

The fallow deer (*Dama dama*) fossil assemblage from Camino Cave constitutes the most numerous and, probably, the most recent known Iberian population of this species.

Despite *D. d. geiselana* and *D. d. tiberina* are not cited for the Late Pleistocene record, morphological and morphometrical analyses indicate that fallow deer from Camino Cave are more similar to these subspecies than to the recent *D. d. dama*. Measurements of the postcranial elements are more comparable to *D. d. geiselana* from Neumark Nord. For these reasons, we classify them as *Dama dama* cf. *geiselana*.

Seasonality indicators suggest that both predators and preys were present during all or, at least, most of the year in the surroundings of Camino Cave.

The ungulate assemblage of Camino Cave evidences temperate environmental conditions and a diverse landscape complex with the presence of forested areas, open grasslands and rocky areas. Pollen, charcoal and small vertebrate analyses reflect a Mediterranean climate in the area, which is in agreement with the paleoenvironmental information provided by the ungulate association. Temperate environments during MIS 5 are also registered at other fossil assemblages from the Iberian Mediterranean margin.

Acknowledgements

This research has been conducted within project S2010/BMD-2330 funded by the I+D activities program for research groups of the Consejería de Educación of the Community of Madrid. The study was also supported by the following organizations: Ministerio de Cultura, Museo Arqueológico Regional de la Comunidad de Madrid, Grupo Mahou and Canal de Isabel II. For information, discussion, and various further support our thanks are due to N. García (Madrid), M. Méndez (Madrid), P. Turrero (Oviedo), S. Bárez (Madrid), C. Laplana (Alcalá de Henares), E. Maldonado (Madrid), J. van der Made (Madrid), A. Lister (London), the members of the Pinilla del Valle excavation team and the two anonymous reviewers who greatly helped to improve the manuscript.

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Table 1. Composition of the Camino Cave ungulate assemblage (data from 2002-2009 excavations).

Taxa	**NISP**	**%** NISP	**MNI**	**%** MNI
Dama dama	635	51.5	27	54
Cervus elaphus	104	8.4	8	16
Dama/Cervus	284	22.9	-	-
Capreolus capreolus	7	0.6	1	2
Bos primigenius	68	5.5	4	8
Rupicapra rupicapra	1	0.1	1	2
Sus scrofa	24	2	2	4
Equus caballus	94	7.6	5	10
Stephanorhinus hemitoechus	18	1.4	2	4
TOTAL	1235	100	50	100

Table 2. Selected comparative measurements of *Dama dama* metapodials.

Population		**Mtc. L**	**Mtc. PW**	**Mtt. L**	**Mtt. PW**
Camino Cave[a,b]	Mean (n)	203.4 (7)	28.8 (7)	243.4 (9)	28.5 (9)
	Min-Max	194-212.2	27.3-32.4	229.3-249	26.9-30.4
D. d. geiselana (Newmark Nord) [c]	Mean (n)	229.2 (29)	33.4 (29)	255.2 (33)	31.4 (33)
	Min-Max	210-243	30-36	235-270	28-36
D. d. tiberina[d]	Mean (n)			253.1 (4)	29.8 (4)
	Min-Max			250-261	29-30.9
D. d. dama (Recent) [c]	Mean (n)	181.2 (39)	28.5 (39)	206.8 (44)	26.5 (44)
	Min-Max	166-196	25.5-33	189-223	23-30.3

Mtc.: metacarpal; Mtt.: metatarsal; L: maximum length; PW: proximal width.
[a] Own data; [b] Buitrago, 1992; [c] Pfeiffer, 1998; [d] Di Stefano and Petronio, 1997.

Table 3. Selected comparative measurements of *Cervus elaphus* M_3 and metapodials.

Site		M_3 L	Mtc. L	Mtc. PW	Mtc. DW	Mtt. L	Mtt. PW	Mtt. DW
Camino Cave[a]	Mean (n)	29.88 (11)	265.6 (3)	40.95 (5)	41.4 (5)	276 (1)	34.47 (4)	41.43 (3)
	Min-max	28.1-32.3	260.9-271	38.2-45.95	38.4-42.8		32.5-34.4	38.4-42.9
Cova Negra[b]	Mean (n)	30 (7)						
	Min-max	25.2-32.8						
Lezetxiki[c]	Mean (n)	32.26 (3)						
	Min-max	28.2-34.6						
Aitzbitatrte IV[c]	Mean (n)	34.6 (6)		47.65 (4)	47.73 (3)			
	Min-max	31.5-36.1		43.2-53.8	45.1-51.1			
Urtiaga D[c]	Mean (n)	34.8 (30)					38.98 (5)	46.65 (7)
	Min-max	30.1-38.1					35.6-44	42.7-53
Morín[d]	Mean (n)	35.27 (14)			43.13 (3)			
	Min-max	31-39.5			40-45,7			
Tito Bustillo[e]	Mean (n)	34.86 (13)			42.76 (15)			44.58 (12)
	Min-max	32-39			40-49			42-49.5
Zatoya[f]	Mean (n)	32.12 (4)						
	Min-max	28-34.5						
Labeko Koba[g]	Mean (n)	32.93 (12)	266.85 (7)	46.35 (7)	48.59 (11)	308.75 (6)	41.41 (11)	49.31 (8)
	Min-max	31-35	254-283	42.5-48	44-51	290-321	37-45	45-50.5
La Paloma[h]	Mean (n)	34.29 (89)		43.91 (6)	42.67 (70)		38.25 (4)	43.66 (43)
	Min-max	29.5-39		37.5-50.5	38.5-50.5		32-43.5	40.5-48.5
Las Caldas[i]	Mean (n)	34.96 (3)						
	Min-max	33.5-36.8						
Romain-la-Roche[j]	Mean (n)	31.8 (4)						
	Min-max	30-33.4						
Lazaret C II[k]	Mean (n)	34.5 (18)						
	Min-max	31.8-38.3						
Piégu[k]	Mean (n)	32.4 (10)						
	Min-max	29.3-37.4						
La Ferrassie[l]	Mean (n)	33.3 (7)						
	Min-max	31-37						
Vaufrey[m]	Mean (n)	32.2 (8)						
	Min-max	28.3-35.1						
Swanscombe[n]	Mean (n)	28 (3)						
	Min-max	27.8-28.3						

Mtc.: metacarpal; Mtt.: metatarsal; L: maximum length; PW: proximal width; DW: distal width.

[a] Own data; [b] Pérez Ripoll, 1977; [c] Altuna, 1972; [d] Altuna, 1971; [e] Altuna, 1976; [f] Mariezkurrena and Altuna, 1989; [g] Altuna and Mariezkurrena, 2000; [h] Castaños, 1980; [i] Soto and Meléndez, 1981; [j] Auguste, 2010; [k] Liouville, 2007; [l] Delpech, 1984; [m] Delpech, 1988; [n] Lister, 1986.

Table 4. Selected comparative measurements of *Stephanorhinus hemitoechus* and *Stephanorhinus kirchbergensis* M^1 and M^2.

Site			L	W
Camino Cave[a]			55.5	65
S. hemitoechus (European sites)[b]	M1	Mean (n)	53.2 (10)	61.09 (16)
		Min-Max	43.5-57.5	53-68
	M2	Mean (n)	59.25 (12)	64.22 (16)
		Min-Max	46.5-65	56-72
S. kirchbergensis (European sites)[b]	M1	Mean (n)	58.3 (5)	67.2 (5)
		Min-Max	52-63.5	60-71.5
	M2	Mean (n)	64.75 (4)	67.57 (7)
		Min-Max	61.5-67	62-72.5

L: maximum length; W: maximum width.
[a] Own data; [b] Guérin, 1980.

FIGURE CAPTIONS

Fig. 1. Situation of Iberian sites of MIS 5 age mentioned in the text. Camino Cave is represented with a black star.

Fig. 2. Site map showing the four sectors defined for the excavated areas and the location of the dating mentioned in the text (a), and stratigraphic section throughout the squares Z6-Z9 (b). Modified from Pérez-González et al. (2010) and Arsuaga et al. (2012).

Fig. 3. Ungulate cranial and postcranial remains from Camino Cave. *Dama dama*: right P^3-M^2 series in occlusal view (a), left P_3-M_3 series in occlusal view (b), right metacarpal in anterior view (c), left metatarsal in anterior view (d). *Cervus elaphus*: right P^3-M^3 series in occlusal view (e), left metacarpal in anterior view (f), shed antler basis in lateral view (g), skull fragment with full developed antler basis in anterior view (h). *Capreolus capreolus*: right mandible fragment with P_4, M_2 and M_3 in lingual view (i). *Bos primigenius*: left P^2-M^3 series in occlusal view (j), right calcaneus in anterior view (k). *Rupicapra rupicapra*: left M_3 in labial view (l). *Sus scrofa*: right mandible fragment with P_3-M_3 series in lingual view (m). *Equus caballus*: right P_2 in occlusal view (n), left M^3 in occlusal view (o), left astragalus in anterior view (p). *Stephanorhinus hemitoechus*: right M^2 in occlusal view (q).

Fig. 4. Plot of the fallow deer metacarpal measurements L (maximum length) and PW (proximal width). Unfilled triangles: recent *Dama dama dama*; unfilled dots: *Dama dama geiselana* from Neumark Nord; black dots: *Dama dama* from Camino Cave.

Fig. 5. Plot of the fallow deer metatarsal measurements L (maximum length) and PW (proximal width). Unfilled triangles: recent *Dama dama dama*; unfilled dots: *Dama dama geiselana* from Neumark Nord; unfilled squares: *Dama dama tiberina*; black dots: *Dama dama* from Camino Cave.

Fig. 6. Estimation of the time of death in 19 fallow deer young individuals from Camino Cave.

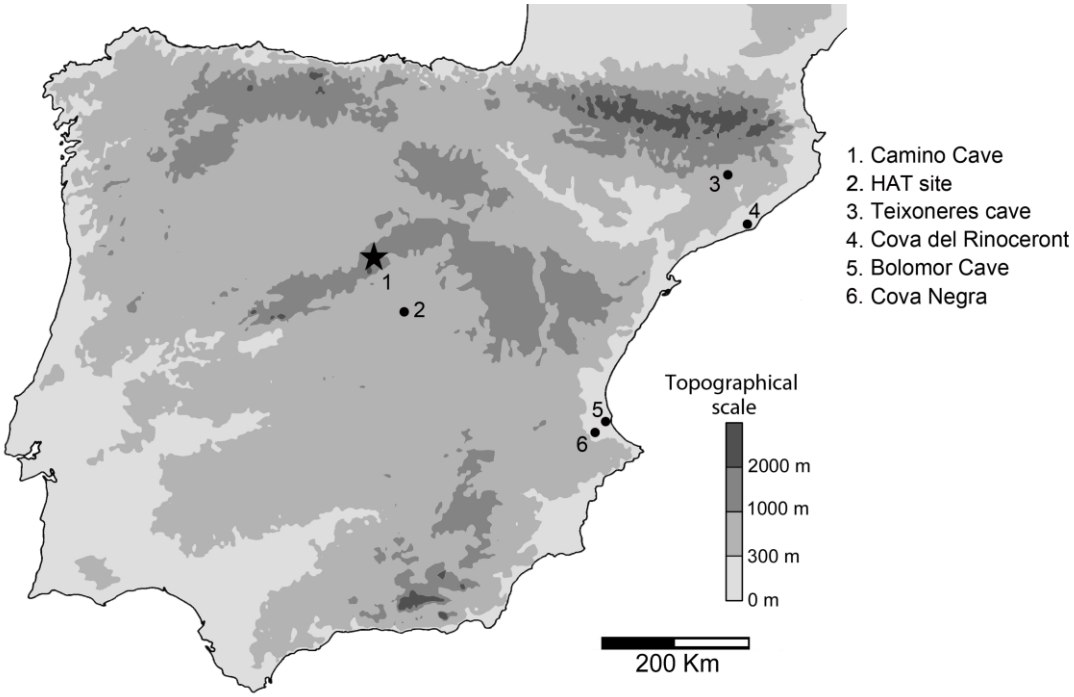

Figure 1

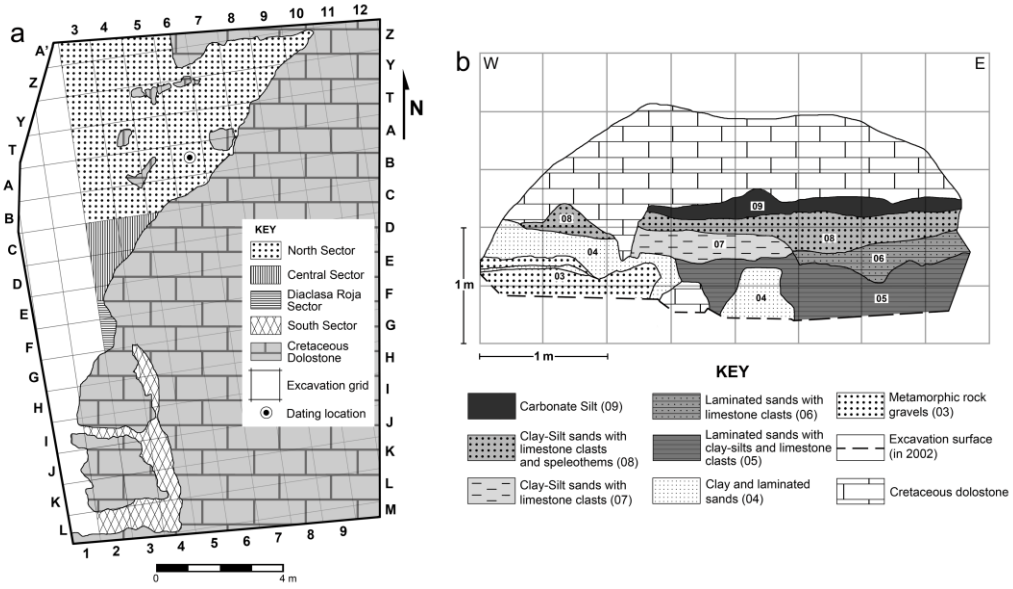

Figure 2

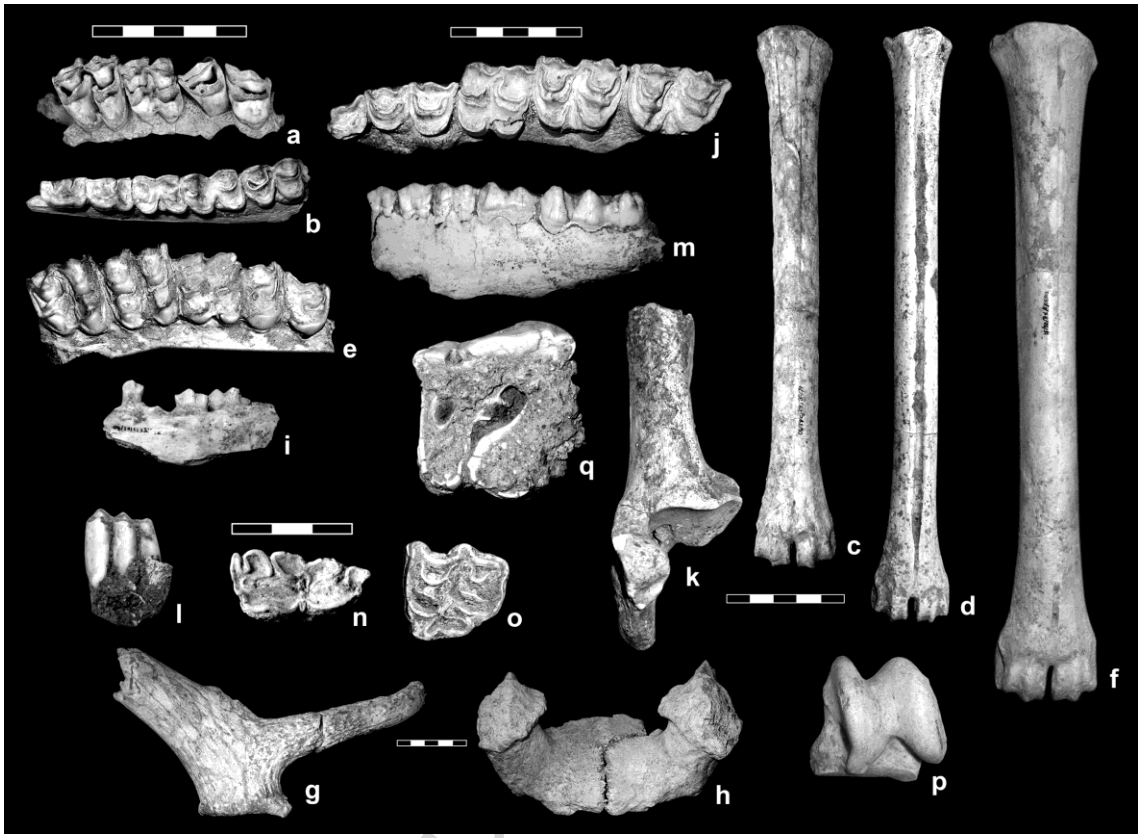

Figure 3

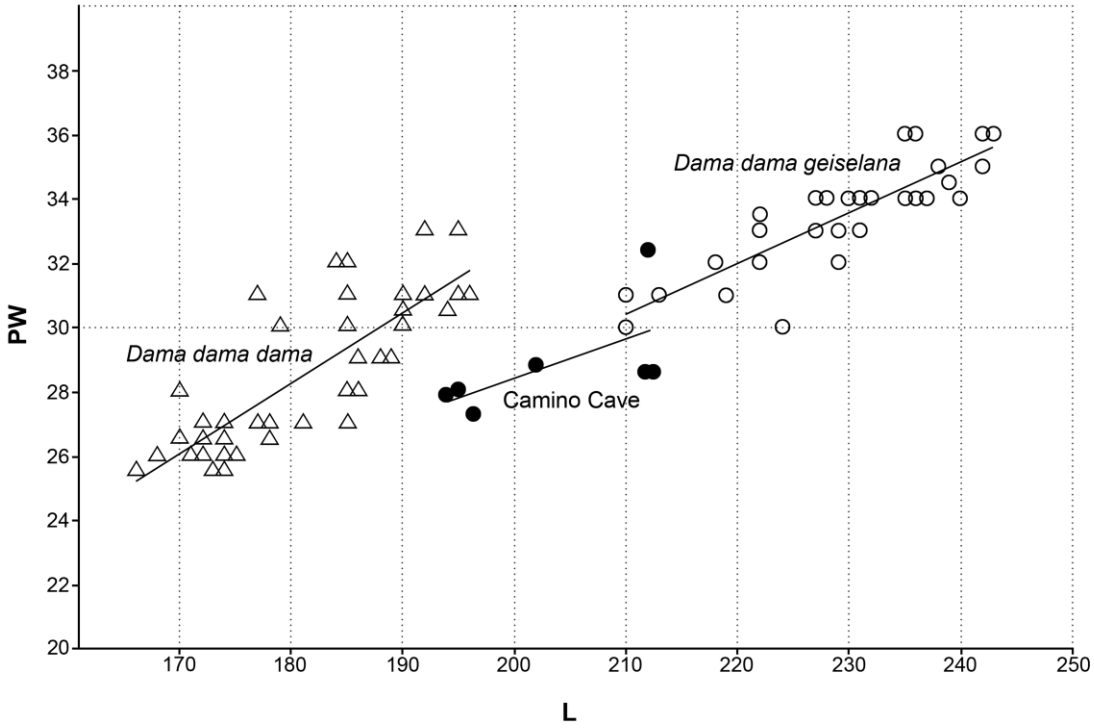

Figure 4

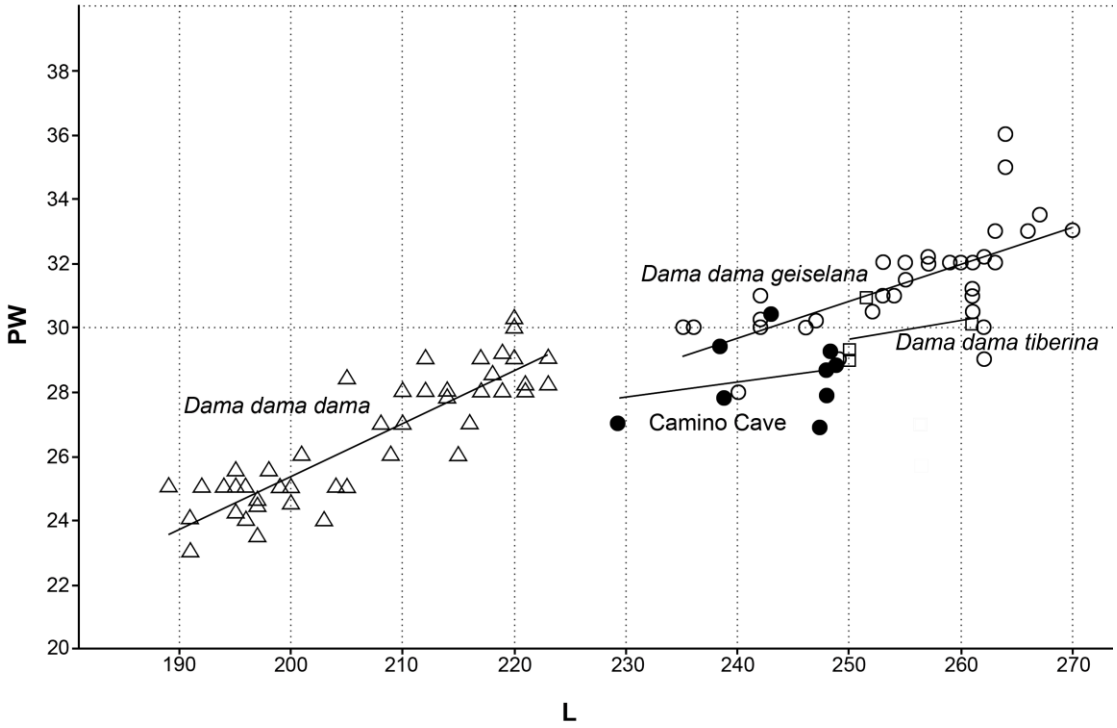

Figure 5

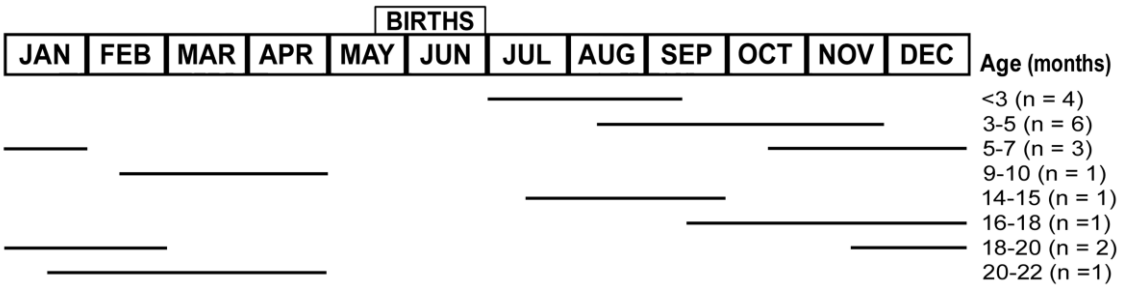

Figure 6

Highlights

>We present the first MIS 5 ungulate assemblage known from Central Iberia. >Camino Cave ungulates represent a typical example of an interglacial faunal complex. >The most numerous Iberian fallow deer fossil population was here recovered. >Fallow deer from Camino Cave belong to the subspecies *Dama dama* cf. *geiselana*.